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ALUMINUM TOXICITY IN CROP PLANTS

Key Words: Al screening methodology, Al species, Al tolerance mechanisms.

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ABSTRACT

Aluminum toxicity can be an important growth limiting factors occurring on acid soils where crop yields may be increased if Al availability is reduced. A combination of liming to reduce plow layer Al plus the selection of plant species or cultivars within species that tolerate high subsoil Al are potential solution. Aluminum toxicity, Al tolerance mechanisms, physiological and biochemical effects of Al on plant growth, plant species tolerance to Al toxicity and methodology for Al screening are discussed.

INTRODUCTION

Aluminum toxicity can be one of the more important growth limiting factors occurring on acid soils. It commonly occurs in Oxisols and Ultisols as well as other heavily leached soils such as the laterites of the humid tropics. Oxisols, Ultisols and Inceptisols of the tropics occupy about one billion hectares. The leached soils of the temperate regions total about 325 million hectares, and the Ultisols equal about 130 million hectares (13). In terms of potential arable land that does not require irrigation, Oxisols, Ultisols and Inceptisols represent 33, 10, and 4%, respectively, of the area. Therefore, nearly half of the nonirrigated arable lands are acid soils with Al toxicity problems, highly weathered soils which are often deficient in Ca, Mg and P. Thus, it is often difficult to separate the effects of Al toxicity from deficiencies of these elements.

Aluminum toxicity reduces both root and shoot growth. Reduction in root growth reduces the aborption of nutrients and water, and consequently, crop yield. Liming, to raise the soil pH can reduce the probability of Al toxicity. Selection of plants tolerant to Al toxicity can be a complementary method to liming to overcome Al toxicity. In addition, varietal differences in terms of Al tolerance have been reported for rice (18,21), corn (12), snapbeans (30), wheat (31), alfalfa (4), tomatoes (27), sunflower (32), sweet potato (45), and soybean (4).

Although there has been much work done regarding Al tolerance of crop plants, there is only speculation about the mechanism of tolerance. It still is not clear which specie of Al is most toxic to plant growth. Much of the crop screening work for Al tolerance has been done under controlled conditions with very little done under field conditions. Therefore, our objective is to evaluate the existing information about Al toxicity in crop plants, the plants that are important food sources, and see how they adapt to this specific elemental toxicity. A better understanding of Al toxicity may offer clues as to how best to solve this problem.

ALUMINUM SPECIES TOXIC TO PLANTS

Although considerable research of Al toxicity in various crop plants has been done (4,7,12,18), considerable uncertainty about the degree of toxicity for the various forms of soil Al. Normally, plant response to Al toxicity has been evaluated by relating plant growth to the total amount applied or to that measured in solution (5,22). The latter may comprise both monomeric and polymeric Al. In the presence of sulfate in solution, and over the pH range of 4 to 6, monomeric Al species are represented by the following equation: (Al monomeric) = $(Al^{3+}) + Al(OH)^{2+} + Al(OH)_2^+ + Al(OH)_3^+ + Al(SO_4)^+$. The concentrations, activity coefficients, and activities of the five monomeric Al species given in the above equation can be calculated by means of the GEOCHEM computer program (53) or by using the equilibrium constants reported by Lindsay (40).

The reactivity of Al in acid soils varies with the form in which it occurs, decreasing in order from water-soluble Al^{3+} or OH-Al monomers to polymerized hydroxy-Al forms. According to McLean (41) the solution chemistry of Al is affected by the pH of the solution. The sequence of the possible forms of Al ions in solution can be represented by the following progression:

Reactions	Soil-Water pH	Al Solubility
$Al^{3+} + H_2O \quad Al(OH)^{2+} + H^+$	≤ 4.0 - 4.5	
$Al(OH)^{2+} + H_2O \quad Al(OH)_2^+ + H^+$	4.5 - 5.5	Increase
$Al(OH)_2^+ + H_2O \quad Al(OH)_3 + H^+$	5.5 - 7.5	Low or none
$Al(OH)_3 + H_2O \quad Al(OH)_4^- + H^+$	7.5 - 9.0	
$Al(OH)_4^- + H_2O \quad Al(OH)_2^- + H^+$	9.0 - 9.5	Increase
$Al(OH)_2^- + H_2O \quad Al(OH)_3^- + H^+$	9.5 - 10.0	

From this sequence, it can be seen that the solubility of Al is quite low within the soil water pH range of 5.5 to 7.5 where it is precipitated and remains as the relatively insoluble $Al(OH)_3$. But below pH 5.5 and above pH 7.5, the concentration of Al in the soil solution increase rapidly.

Since Al can exist in a variety of forms, only some of these forms are toxic to plants. Organically complexed and polynuclear forms of Al are generally thought to have little, if any, phytotoxicity (35). The inorganic Al monomers, including Al^{3+} and hydroxy-Al species, have generally been regarded as the toxic forms of Al in aqueous systems (5). General agreement does not exist as to the relative toxicity of the inorganic monomeric Al species. Cameron et al. (11) and Kinraide and Parker (38) have recently demonstrated that SO_4 and F complexes of Al do not exhibit root elongation. The relative toxicity of Al^{3+} and the hydroxy-Al species, however, is in doubt. Initially, investigators assumed that Al^{3+} was the most toxic species for crop plants (2). According to Blamey et al. (9), either Al^{3+} or $Al(OH)_2^+$ species are predominantly responsible for decreases in soybean root growth. Similarly, Pavan and Bingham (49) suggested that root growth of coffee in nutrient solution at pH 4 $\pm$ 0.2 was more closely associated with the calculated activity of Al^{3+} than with the activity of other monomers in the root environment. Fageria et al. (24) found similar relationships between calculated activities of Al monomers and growth of rice in nutrient solution at pH 4 $\pm$ 0.2. On the other hand, Kerridge (37) reported that a hydrolysis product of Al is more toxic to wheat than Al^{3+}. Similarly, Moore (44) reported that $Al(OH)^{2+}$ was the monomer responsible for toxicity rather than Al^{3+} at pH 4.5.

According to Alva et al. (5), among the individual Al monomers, relative root length of soybean was most highly correlated with calculated activity of $Al(OH)^{2+}$ followed by $AlSO_4^+$, $Al(OH)^+$, and Al^{3+}. They also found through reinterpretation of data from other studies with soybean, subterranean clover, alfalfa, and sunflower that root growth was most highly correlated with activities of $Al(OH)^{2+}$ or $Al(OH)_2^+$ (4). In the majority of cases, the relationship between root growth and activity of Al^{3+} was relatively poor. This situation is further complicated by the fact that Ca and other cations, as well as pH, influence the expression of Al toxicity (11,38).

MECHANISMS OF ALUMINUM TOLERANCE

The exact mechanisms by which certain plants tolerate high levels of Al is still debated. Several hypothesis have been suggested but much research remains to be done to verify these hypotheses. The following are the current hypotheses:

1. Tolerant plants either prevent excess Al absorption by the roots or detoxify Al after it has been absorbed (25).

2. Tolerant plants or cultivars have higher rates of root growth, thereby uptake of water and nutrients is greater (18).

3. Aluminum tolerant plants may have higher cellular respiration which reverses the uptake of all ions (3).

4. Aluminum tolerant cultivars increase the growth medium pH and thus, reduce Al solubility and toxicity. In contrast, Al sensitive cultivars of the same species lower the pH of the growth medium, thereby increasing Al solubility and toxicity (25).

5. Aluminum increases the viscocity of protoplasm in plant root cells and decreases the overall permeability to salts. Tolerant cultivars have reduced viscocity as compared to sensitive cultivars (3,43).

6. Aluminum blocks, neutralizes, or reverses the negative charge on the pores of the free space and thereby reduces the ability of such pores to bind Ca (15). This may vary from cultivar to cultivar.

7. Aluminum tolerant species may control excess Al in roots and restrict its transport to shoots (22).

8. Aluminum tolerant plant species contain high levels of organic acids that chelate and detoxify Al within the plant (25).

9. Aluminum tolerance in some plants is associated with their ability to absorb and metabolize P (8,20).

10. Aluminum tolerant plant species have a higher root-phosphatase activity and absorb low levels of organic or inorganic P more efficiently than Al sensitive plants (14).

11. Superior Al tolerance in certain pasture species coincides with more efficient uptake and transport of P and Ca (7).

12. Aluminum tolerance among certain cultivars of wheat, barley, and soybean is associated with their ability to resist Al-induced Ca deficiency or Ca transport difficulties (25).

PHYSIOLOGICAL AND BIOCHEMICAL EFFECTS OF ALUMINUM

Excess Al in the growth medium influences several physiological and biochemical processes in plants which, in turn, affect their growth and development. The more important processes affected by excess Al are:

1. Interference with cell division in root and lateral roots (47).

2. Increases in cell wall rigidity by cross-linking pectins (26).

3. Reduced DNA replication by increasing the rigidity of the DNA double helix (55).

4. Root membrane structures and functions are altered (33).

5. Enzymes governing sugar phosphorylation and the deposition of cell wall polysaccharides are interferred with (26).

6. Cell permeability is decreased through protein coagulation inhibited cell division (26).

7. Uptake and utilization of most of the essential nutrients is inhibited (20,22).

8. Growth of roots and shoots is reduced (17,18,29).

9. Aluminum interferes with water use by plants which then results in reduced crop yields (34,36).

10. Reduced root respiration which consequently, reduces uptake of water and nutrients (39).

11. Precipitation of nucleic acid by forming strong complexes (54).

12. An abnormal distribution of ribosomes on the endoplasmic reticulum of root cells results and interfere with protein synthesis (42).

13. Increased firmness and decreased solubility of protein/case in fibers in legumes (52).

14. Trivalent Al coordination forms complex with carboxyl and sulfhydryl groups of proteins producing cross linkage (27).

15. Aluminum binds to either proteins or lipids, depending on pH and other conditions (56).

<u>PLANT SPECIES TOLERANT TO ALUMINUM TOXICITY</u>

It has been shown that plant species and cultivars within species differ greatly in their tolerance to Al stress (6,14,23, 49). Some of those crop species tolerant to Al are given in

Table 1. In addition to these species, differential Al tolerance among cultivars of barley, wheat, alfalfa, tomato, soybean, snapbean, sunflower, pea and sweet potato have been reported (25,26). Plant, soil, and climatic factors also determined the tolerance of a particular plant species to Al toxicity. Native plant species have always had higher adaptability than newly introduced species, with native plants having a lower capacity to respond to improved cultural practices. Therefore, in any plant selection program for elemental stress, local plant species can provide a good source of resistance in breeding programs.

METHODOLOGY FOR Al SCREENING

Numerous methodological problems frequently make a probable explanation of results obtained in genotype screening very difficult. There are several useful techniques that have been used for Al stress screening (6,29,46,50), using either solution systems as well as some soil procedures.

Within these mediums, various concentrations of nutrients, volumes of solution and different types of soil have been used. All these factors make comparisons of experimental results difficult and more complex. Therefore, experimental conditions need to be standardized as much as possible when screening genotypes for Al stress or other elemental stress problems. The following are recommended screening procedures:

1. Standardized growth medium and ecological conditions.
2. Use of genotypes with the same growth cycle.
3. Well-defined evaluation parameters.
4. Screening techniques that permit evaluation of a large number of materials with reasonable precision.
5. Use of an appropriate site or soil deficient or toxic in nutrients and/or element under study.
6. Established minimum and maximum nutrient levels.
7. A minimum of three Al levels spacing the expected response range.

TABLE 1.
Aluminum Tolerant Plant Species

Common Name	Scientific Name	Reference
Azalea	Azalea Sp.	26
Datura	Datura Sp.	26
Rye	Secale cereale	26
Cranberry	Oxycoccus Sp.	26
Tea	Thea sinensis	26
Bermudagrass	Cynodon dactylon	26
Stargrass	Aletris farinosa	26
Buckwheat	Fagopyrum esculentum	26
Peanut	Arachis hypogea	26
Pangolagrass	Digitaria decumbens	10
Rubber	Hevea brasiliensis	51
Blueberries	Vaccinium Sp.	16
Norway Spruce	Picea obies	48
Rice	Oryza sativa L.	20

8. Verification of greenhouse results under field conditions and vice-versa.

9. When screening for determined nutrient efficiency, other nutrients present should be at levels expected and with normal ranges.

10. Tolerant and susceptible cultivars should be included in all the genotype screening studies.

11. All plant material should be genetically uniform.

12. For improved applicability of screening results, plants should be allowed to grow in the stress medium at least 3 to 4 weeks. Short-term experimental studies only account for the effects of Al on root elongation and cell division, while longer term experimental results reflect the continued effect of Al on root growth, as well as shoot growth and nutrient uptake.

Aluminum is generally the major toxic component in acid soils, although Mn can also be a factor. A simple field screening method has been developed at the National Rice and Bean Research Center of EMBRAPA, Goiania, Brazil to permit efficient screening of crop lines or cultivars for Al tolerance (23). According to this method, grain yield is related to soil Al saturation at the flowering stage of the crop specie evaluated. Two levels of Al saturation are created (i.e. low and high).

TABLE 2
Critical Toxic Level of % Saturation of Al in soil for Important Field Crops (19).

Common Name	Scientific Name	Critical Al Saturation %
Rice	Oryza sativa L.	> 45
Corn	Zea mays L.	30
Wheat	Triticum aestivum L.	30
Barley	*Hordeum vulare L.*	30
Common Beans	Phaseolus vulgaris L.	20
Soybean	Glycine max L. Men	20
Oat	Avena sativa L.	15
Alfalfa	Medicago sativa L.	15
Cotton	Gossypium hirsutum L.	10

The effect of high Al levels vary from one crop species to another. An approximate high Al saturation index for some important crops is given in Table 2. It can be seen that toxic Al levels for any given species cover a considerable range. Tolerance to the Al toxicity (Al_t) was calculated as follows:

$$Al_t = \frac{\text{Yield at low level of Al - Yield at high level of Al}}{\text{Al saturation of unlimed soil-Al saturation of limed soil}}$$

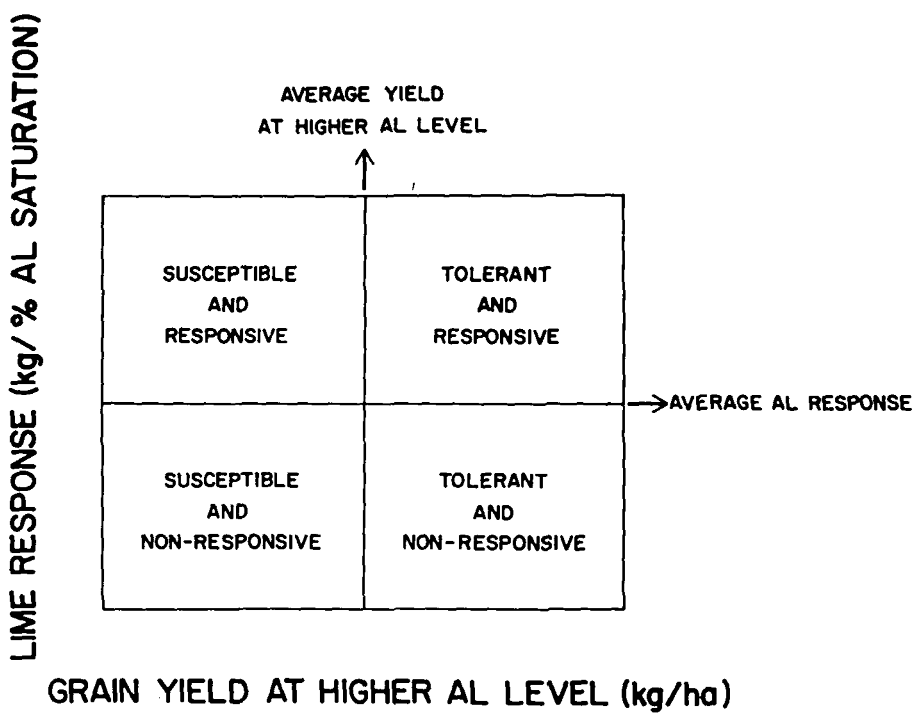
The grain yield from high Al plots and Al_t are plotted on the x and y axes, respectively (Fig. 1). The average yield at the high Al level and Al_t are calculated which formed the basis to divide the diagram into gradients representing the four categories of cultivars described as either:

1. Tolerant and Responsive (Cultivars that yield well under the high Al level and respond well to added lime), or

2. Tolerant and Nonresponsive (Cultivars that produce well under the high Al level, but do not respond to added lime), or

3, Susceptible and Responsive (Cultivars that produce less under high Al levels, but respond to added lime), or

4. Susceptible and Nonresponsive (Cultivars that perform poorly under high and low Al levels).



Upland rice cultivars were screened for Al tolerance at the National Rice and Bean Research Center, Brazil, using this methodology and results are presented in Table 3.

When this methodology can be used under greenhouse conditions, it is not necessary to use grain yield as a criteria as dry matter can be used as a parameter to save growing time. However, whatever method of evaluation is used, it is advisable to include some reference standards, cultivars that are known as either susceptible or tolerant in the study for comparative purposes.

TABLE 3

Classification of Upland rice cultivars/lines to aluminum toxicity.

Cultivar/Line	Yeald at Low Al Saturation	Yield at High Al Saturation†	Lime Response kg/% Al Saturation	Classification
CNA790318	3055	2720	7.4	TNR
CNA790678	3390	2473	20.4	TR
IAC47	2221	1631	13.0	TR
CNA800056	2023	1543	10.7	SR
CNA790278	2378	2353	0.6	TNR
CNA800160	2339	2121	4.8	TNR
CNA800045	3043	2777	6.0	TNR
CNA790261	2800	2558	5.4	TNR
CNA791024	1995	1200	17.7	SR
CNA790241	1601	1095	11.2	SR
CNA770646	1685	1198	10.8	SR
CNA790035	1073	435	14.2	SR
IRAT144	1097	1059	0.8	SNR
IAC164	1004	753	5.6	SNR
L-45	978	738	5.3	SNR
IAC165	807	532	6.1	SNR
Average	1931	1611	8.8	

TNR = Tolerant and nonresponsive: TR = Tolerant and responsive, SR = Susceptible and responsive, and SNR = Susceptibe and non-responsive.
†Aluminum saturation was 60 and 15% in the unlimed and limed plots, respectively.

CONCLUSION

Aluminum toxicity exists in many soils throughout the world, a vast area of land that can be made much more productive if Al toxicity were reduced. Liming is the most common practice to alleviate or reduce Al toxicity. Since genetic Al tolerance variability does exist in crop plants, perhaps the best solution for overcoming Al toxicity would be a combination of both liming and selection of Al tolerant plant species, or cultivars within a species. However, more information is needed on the plant component of this approach, especially a better understanding of

Al tolerance mechanisms and how there can be incorporating into productive cultivars. It is essential that there be cooperation among plant nutritionists, breeders, soil scientists, agronomists, and plant physiologists if this multidisciplinary approach is to bring fruitful results in solving this elemental toxicity.

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